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EVOLUTION OF THE BASAL PLATES IN MONOCYCLIC CRINOIDEA CAMERATA. I

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PART I

INTRODUCTION

Most students of fossil crinoids have been interested in the morphological results of evolution rather than in the morphological processes of evolution and their results, and the description of extinct, fossil crinoids as well as of most living ones has been in general a tabulation of those results. In many cases the tabulation is incomplete, not only because of the rarity and incompleteness of the specimens described, their poor preservation and sometimes poorer preparation, but also because the obscure morphological processes which have given rise to their characteristics are either overlooked or misinterpreted. The greatest difficulty in establishing a natural classification lies in the fact that processes giving rise to morphological characteristics must be known before a correct interpretation and classification can be made. From necessity paleontologists are familiar with the obscurity of processes. The ontogeny of the fossil crinoid is only partially revealed, and that mostly in the phylogenetic succession, for the delicately constructed embryos are ill-adapted for preservation, and comparatively few immature individuals have been preserved. The complete embryonic and larval development of modern crinoids is known only in one highly specialized genus, *Antedon;* the larval stages, however, are partially known in four other genera, *Promacocrinus*, *Thaumatocrinus*, *Comactinia*, and *Hathrometra*.

Various phases of the evolutional changes in the basal plates of crinoids have been considered by both paleontologists and zoölogists. The relation of these plates to the column, their modification by the anal plate, and their characteristic decrease in number and size with the passage of geologic time attracted attention long before the importance of tegminal structure was realized,[1] and some interesting though unsuccessful attempts have been made to use basals as a foundation for classification.[2] Such artificial classifications have been swept away, but the fact remains that the changes of each plate and system of plates, as they have passed through the varying stages of evolution, must have classificatory value. When, where, and from what the monocyclic Crinoidea originated are questions of great importance, yet not of special import for the subject as herein discussed. The fact that monocyclic crinoids have existed, that their basal plates exhibit a series of remarkable changes, and that certain features in their phylogeny throw much light upon the character of the changes and their succession, is sufficient for present purposes. The process by which these changes came about is the problem to be considered here.

In this paper no attempt at reclassification will be made, but the changes exhibited by the basal plates will be reviewed, the nature of these changes studied, and suggestions arising from these studies will be applied to certain theories of descent that have arisen from similar studies made by others.

ACKNOWLEDGMENTS

The writer desires to express his sincere appreciation to Professor Stuart Weller, of the University of Chicago; Mr. Frank Springer, Mr. Austin Hobart Clark, Dr. E. O. Ulrich, and Dr. R. S. Bassler, of the United States National Museum; and to Professor R. A. Budington, Dr. Charles G. Rogers, and Dr. Maynard M. Metcalf, of Oberlin College, for the material assistance given by them in the use of specimens and literature, and for a broad view of the

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[1] Ref. 38. (The reference figure is the number assigned to the work cited in the Bibliography.)

[2] Ref. 2; ref. 22.

processes operative in the growth and modification of many groups of invertebrates.

To Professor Weller, Mr. Springer, and Mr. Clark the writer is especially indebted for their many kindnesses, their helpful advice, and the privilege of freely studying their collections of fossil and recent crinoids.

REVIEW OF WACHSMUTH AND SPRINGER'S THEORY OF BASAL PLATE EVOLUTION

While various phases of basal plate evolution have been touched upon by numerous writers, the discussion by Wachsmuth and Springer[1] is the only one in which a general treatment of the subject has been undertaken, and, in order that the reader may have their theory clearly in mind before going farther, it will be quoted in substance.

The base of a monocyclic crinoid is composed of a single cycle of plates, termed the basal plates, lying at the proximal end of the cup, between the stem and the first plates of the radial series. This plate cycle was primarily composed of five separate plates, but, by anchylosis or the union of two or more members, they were reduced from five plates to four, three, two, or one. The first monocyclic crinoids had five basals.

> Before the close of the Lower Silurian (Ordovician) there appeared two monocyclic genera with four basals, both having a special anal plate interposed between the radial. The quadripartite base reached its culmination in the Upper Silurian (Silurian), and disappeared before the close of the Devonian. The earliest genera with a tripartite base occur in the Upper Silurian; some of them have an anal plate, and others not. When that plate is represented, the basals are of equal size; when absent, two of the basals are equal, and the third about half smaller. The two forms continue to exist side by side to the end of the St. Louis group of the Carboniferous (Mississippian) when both became extinct. The bipartite base is restricted to the Carboniferous (Mississippian and Pennsylvanian). It occurs from the Kinderhook group up to the Coal Measures, but is found only among genera with a large[2] anal plate.

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[1] Ref. 39, pp. 52–68.

[2] The exact meaning of the statement that the bipartite base is found only among genera with a large anal plate is doubtful, as *Pterotocrinus*, a genus with a hexagonal bipartite base, usually has, in proportion to the size of its basals and radials, the

It is evident from these observations that the number of basals was gradually reduced in Paleozoic times, and that in the Camerata the anal plate was introduced after the quadripartite base had made its appearance. It will now be shown that this diminution of number was the result of fusion of two or more of the five original plates, and that by the introduction of the anal plate the base underwent further modifications. The manner in which the modifications in the number of basals were effected may be best understood by reference to the diagrams on Table A. [This table is photographically reproduced as Fig. 1 of this article.]

Looking at these diagrams, the transmutation in the Camerata from five basals to a less number is readily understood among genera in which the anal plate is wanting. When the base is quadripartite, it is invariably the two anterior plates of the elementary five which are consolidated (2). In the tripartite base there is a fusion of the posterior with the left postero-lateral basal, and another between the right posterior and the adjoining antero-lateral plate (3). The figure shows that a bisection of the two larger plates will reproduce the original five pieces, interradially disposed.

The case is not so simple in genera with an anal plate, where the form of the basal disk is changed from pentagonal to hexagonal (4), as a bisection of

smallest anal plate now known among Camerata in which the anal plate is in apposition with the base. See Pl. III, No. 11, and Ref. 39, Pl. 79, Figs. 2–9.

When preparing figures for this paper from specimens in Mr. Springer's collection, with his permission, I overlooked the fact that the dorsal cup of this species had never been described or figured. As to this, Mr. Springer has furnished me the following note:

"When proposing the species *Pterotocrinus coronarius* (*Geology of Kentucky*, III, 476, Pl. I, Figs 1*a*, *b*) Lyon described and figured only the tegmen with the ponderous wing plates, as did Wachsmuth and Springer after him (*N.H. Crin. Cam.*, p. 795). While this work was in press I discovered in the Museum of Comparative Zoölogy at Harvard a lead cast of what was apparently the same specimen, with the dorsal cup attached, which fact I mentioned in a footnote on the page cited. When I acquired in 1903 the collection of the late Col. Sidney S. Lyon, I found associated with the tegmen constituting the published type the dorsal cup reproduced in the cast; the two parts were separated, but I have again united them. It is probable that they belong to the same specimen, and the fact that they pertain to the same species is proved beyond question by another specimen from the same locality having the same dorsal cup with one of the wing plates attached. The species is remarkable, not only for its extraordinary wing plates, but also for the construction of the dorsal cup, in which the basal plates are very small and flat, while the radials are of enormous size, larger than all the other plates of the cup combined; this being the reverse of the structures in *Pt. capitalis* and all other known species of the genus. It occurs in the Birdsville formation of the Kaskaskia group, in Crittenden County, Kentucky, where it is extremely rare; and also in the Renault formation in Monroe County, Illinois, from which region a fragmentary specimen was described by Hall (*Geol. Iowa*, II, 689, Pl. XXV, Fig. 7) under the name *Dichocrinus protuberans*."

the larger plates would produce six plates instead of five. This difficulty, however, is overcome if we consider that the introduction of the anal plate into the ring of radials necessitated corresponding modifications among the basals, as otherwise these plates would lose their interradial position. It required either the introduction of a basi-anal plate, or an increase in the size of the original pieces. That the latter occurred among the Camerata is clearly shown by the diagrams, and the evidence leaves no doubt at what part of the base the extra width was inserted.

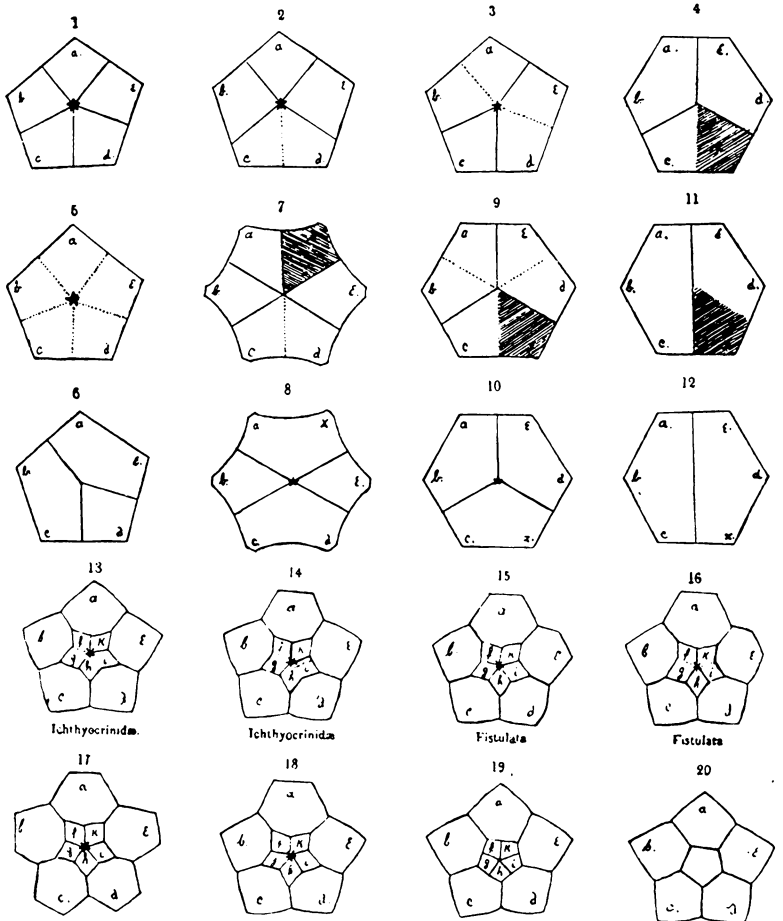

FIG. 1.—Diagrams illustrating the evolution of the basals and infrabasals: all figures represent the anal side at the top; *a* = posterior basal; *b* and *e* = postero-lateral basals; *c* and *d* = anterior basals; *f*, *g*, *h*, *i*, *k* = infrabasals.

> Taking first the quadripartite base, and comparing 2 of the diagrams with 8—one pentangular, the other hexangular—we find that in the latter the posterior basal has doubled in size (7), without materially changing the orientation of the plates, or disturbing their general arrangement. . . . .
>
> In the tripartite base the change was accomplished in a different way. There *x* is added to plate *c* (9 and 10), and plates *ab* and *ed* have coalesced, and hold relatively the same position as in 3.
>
> The bipartite base is probably derived from the tripartite (4), which preceded it in time, and *x*, which in the latter constituted a part of *c*, is united with *de*, and *ab* with *c* (11 and 12).
>
> Now taking up 7 and eliminating *x*, so that the side of plate *a* rests against the plate *e*, we obtain 2, and by a similar procedure we are enabled to transform 9 into 3. The hexagonal base is thus restored to its primitive pentagonal form without disturbing the orientation of any plate, compound or simple.

This theory was thought by Wachsmuth and Springer to have been confirmed by an abnormal example of *Teleiocrinus umbrosus* n which the anal plate was wanting.

> *Teleiocrinus umbrosus* has normally three equal basals, but in this specimen the basal plate to the left of the anterior ray is reduced to one-half its normal size, leaving the basal disk exactly like that of forms which are normally without the anal plate.
>
> It is very remarkable that while in all crinoids with an unequally tripartite, monocyclic base, the smaller plate is located to the *left* of the anterior radial, this plate in the base of the blastoids lies invariably to the *right* (6).

In the discussion of the changes from the pentagonal, five-basal form to the hexagonal, four-basal form, it is stated that the enlargement of the posterior basal took place upon the right side of that plate, but no evidence is submitted for this statement. Why could not the enlargement have taken place as well upon the left side, or by symmetrical development upon both sides of the posterior basal? The statement that "the evidence leaves no doubt at what part of the base the extra width was inserted" is not sufficient, and it in itself creates a doubt. Again we are told that "the introduction of the anal into the ring of radials necessitated corresponding modifications among the basals, as otherwise these plates would lose their inter-radial position."[1] However, in the discussion of the basals in dicyclic crinoids the statement is made that "the introduction of the anal plate into the ring of radials did not affect the basals of dicyclic crinoids" in the same manner as in the monocyclic. While in the latter, when the plate is represented, the orientation of the basals is slightly disturbed, in the dicyclic forms it remains unaltered. The anal plate of the latter rests invariably upon the trunkated upper face of the posterior basal; while in monocyclic crinoids it is supported by the basals *a* and *e* (Nos. 10 and 12), or occasionally by *a* and *x* (No. 8).

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[1] Ref. 39, p. 59.

This statement leads one to believe that no widening of the posterior basal took place upon the introduction of the anal plate in the dicyclic form, but Nos. 15–18 in Fig. 1 show a decided widening of that plate. Overlooking this inconsistency and the fact that trunkation of the posterior basal is in itself an alteration, we are still unenlightened as to why alteration is demanded in the one case and not in the other, as no explanation of an alternative phenomenon is given. Neither is any reason given, other than the position of sutures, for the markedly different positions of enlargement in basal plates of the four-, three-, and two-basal hexagonal forms. By reading between the lines one is able to supply various explanations, yet they are not the explanations of the writers, nor what is needed and demanded by the conditions of the problem. Furthermore, no reasons nor illustrations are given showing why the abnormal specimen of *Teleiocrinus umbrosus*, by which the theory was apparently confirmed, was oriented with the smaller basal in the left anterior interray. The questions in the writer's mind are: Why should the stimulus of enlarging the anal area in the quadripartite form cause enlargement of the right side of the posterior basal and not of the left or of both sides as well? Why should the same stimulus in a dicyclic crinoid have no effect upon the adjacent basal plates? Why should the same stimulus cause the enlargement of the left anterior basal in the equibasaled, tripartite form, and of the left side of the right anterior basal in the equibasaled, bipartite form, derived therefrom? What was the nature of the change in shifting factor *x* from basal *c* to basal *d?* How could such changes take place without disturbing the orientation of any plate, compound or simple? What were the reasons for the orientation assigned to the abnormal specimen of *Teleiocrinus umbrosus?* These questions have led the writer to investigate the evolution of the basal plates in the monocyclic Crinoidea, and the result of this investigation will be stated in the latter part of this study.

REVIEW OF CERTAIN PHYLOGENETIC CHARACTERISTICS IN MONOCYCLIC CAMERATA

In this review the phylogenetic characteristics of the various groups of monocyclic Camerata will be considered, for it is in this order that the succession is better understood and that the evolution of the basal plates is the most complex. There exist in this order two great groups, separated structurally but not phylogenetically according to the outline of the basal cup, and therefore according to the presence or absence of an anal plate in contact with and trunkating the posterior basal. The first of these groups possesses an anal plate in apposition with the posterior basal, and has in consequence a hexagonal basal. The second group, in which plates of the anal series are either present or absent but not in contact with the posterior basal, has a pentagonal base. In considering these facts, questions of descent and relationship necessarily arise.

In the ontogenetic development of the external skeleton in the living *Antedon*[1] so many of the phylogenetic steps found in fossil crinoids are illustrated, that it may well be looked upon as a key to their methods of development and perhaps to their interrelationships. Leaving out of consideration the earlier embryo-logical stages, let us follow in detail the methods of plate intercalation and development after the formation and contact of the basal and oral plates (Fig. 2).

About the time of the attachment of the pentacrinoid larva, the basal plates assume a regular, trapezoidal outline, the lower part of each being an acute-angled triangle with its apex distally directed (Fig. 2, No. 1). The sides of the lower triangle are bordered by a somewhat thickened edge of solid, transparent stereom, the presence of which indicates that the plate has received its full proportionate increase in that direction.[2] Even after the plate edges are thus defined, the plates steadily increase in size, apparently by interstitial growth.[1] The adjacent borders of the plates, however, do not come into absolute contact, as a thin lamina of sarcode is interposed between them until the sutures are closed by anchylosis. The upper margins of the basals have at this time no distinct border,[2] but are still growing by the process of branching and anastomosis (see p. 501, plate growth).

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[1] *Antedon*, while more highly specialized in its larval development than some of the other modern crinoids, is chosen for comparison with the Camerata because it is the best known of any of the genera in which the larval development has been studied.

[2] Ref. 11, p. 729.

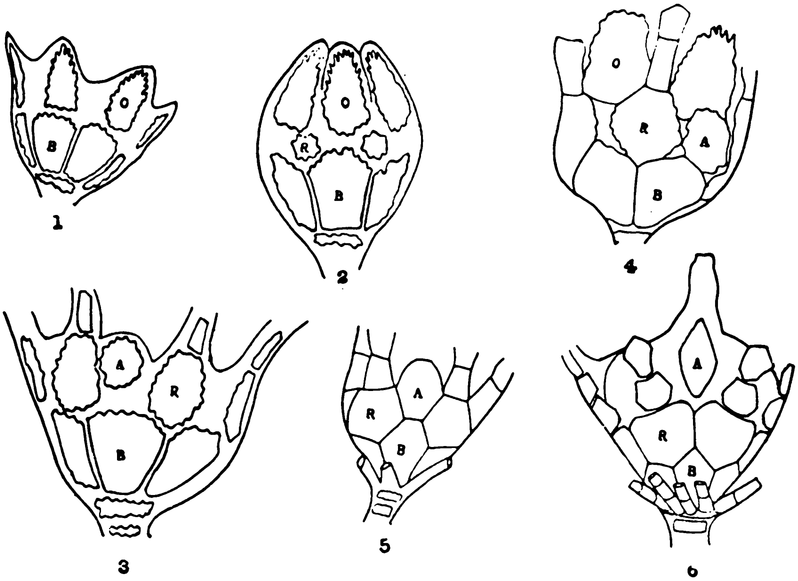

FIG. 2.—Formation of the dorsal cup and migration of the anal plate in *Antedon rosaceus:* 1, 2, after Thomson; 3–5, after Carpenter; 6, original from specimen in Oberlin College Museum; *o*=orals; *b*=basals; *r*=radials; *a*=anal.

Shortly after the fixing of the pentacrinoid and the opening of the cup, a third series of plates, the radials, make their appearance in the space left by the beveling off (absorption) of the adjacent lateral angles of the basals and orals (Fig. 2, No. 2),[3] the beveling being caused apparently by the encroachment of the radials.[4] About the period of the development of the second radials (costals) a forked spicule makes its appearance between the upper parts of the posterior radials. This plate gradually increases in the regular way (see p. 502), until it develops into a round, cubiform plate, the anal plate (Fig. 2, No. 3).[1] The radials, with the anal plate between, now form nearly a complete circle, resting on the basals and separating them completely from the orals.[2] Although greatly enlarged, the radials are still subquadrangular in outline, the proximal angle occupying the enlarged portion of the interbasal suture, and the distal angle, now trunkated, supporting the narrow costals.[3] Considerable space still exists between the adjacent radials, except where they are in apposition with the anal plate (Fig. 2, No. 4), and these spaces are filled only with sarcodic substance.[4] The anal plate from proximal growth now comes into apposition with the posterior basal, and the two are mutually trunkated. Upon further development the radials meet, and their margins assume the finished appearance previously noted in the proximal portion of the basal plates. The posterior radials, especially the right, however, show marked asymmetry, owing to the non-development of the sides adjacent to the anal plate (Fig. 2, No. 5). Growth in the radials does not cease upon their meeting, and as the basals do not now further enlarge, the radials and the anal are forced by contact with each other to extend themselves in an oblique direction, thus enlarging their distal perimeter, and increasing the diameter of the tegmen.

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[1] Interstitial growth: ref. 35, p. 538.

[2] Ref. 11, p. 729, Pl. 41, Fig. 1, *b*.

[3] Ref. 35, p. 539.

[4] Ref. 11, p. 729.

The anal plate by this time has reached its full development and, being more firmly attached to the visceral mass than to the adjacent radials,[5] is gradually lifted out of the cup by the extension of the anal tube. The space left by the withdrawal of the anal is gradually filled by lateral growth from the adjacent radials, which, however, do not immediately come into contact. Before the anal is completely withdrawn from the radial cycle, however, the posterior radials meet below it, and, as withdrawal continues, corresponding and continuous enlargement of the radials fills the re-entrant angle, and gives to the plates their bilaterally symmetrical outline (Fig. 2, No. 6).

About this time a very remarkable change takes place in the tegmen. The oral cycle, like the basal one, does not partake of

[1] Ref. 35, p. 529 (anal).

[2] Ref. 15, p. 314 (radianal).

[3] Ref. 11, p. 729.

[4] Ref. 11, p. 729.

[5] Ref. 11, p. 732.

the pronounced enlargement noted in the radial cycle, its diameter being neither increased by growth of its component parts nor augmented by their separation from one another; but, as the ventral disk expands, the orals become separated from the radials upon which they were previously superimposed and are carried upward and relatively inward and the costals and lower distichals are incorporated into the cup. The space now existing between the radials and orals generally remains as a simple, membranous perisome, traversed by the five ambulacral canals; but, in some specimens of *Antedon rosaceus*,[1] and in other modern crinoids, well-defined groups of interradial plates develop in the angles between the brachials. When these plates appear in the cup they are known as interbrachials, and in the tegmen as interambulacrals. Further tracing of the development of the basals and the orals and consideration of stem formation are not here necessary, although they may at times be referred to in the following discussion.

In tracing the phylogeny of the Batocrinidae and Actinocrinidae, the anal plate is found as a constant characteristic and the base throughout the series is hexagonal. Complete incorporation of the ambulacral grooves has taken place in the tegmen, and the arms are incorporated in the cup up to and often beyond the second distichals. In *Tanocrinus*, a genus probably closely related to the ancestors of the Batocrinidae,[2] five basals are present; the anal plate separates the posterior radials, and is in apposition with and trunkates the posterior basal.

In *Xenocrinus*, *Comprocrinus*, and *Abacocrinus* only four basals are present, the anterior pair being obviously united and somewhat reduced in width. In the other genera of the Batocrinidae and Actinocrinidae there are three equal basals, the basal sutures meeting the antero-lateral radials and the anal plate. Why the third basal suture meets the anal plate will be considered later (Plate III).

The Melocrinidae, while not showing as complex a basal evolution as that shown in the hexagonal Camerata, are interesting in showing the absence of an anal plate in contact with and trunkating the posterior basal, and in some genera an absence of all plates of

[1] Ref. 35, p. 540.

[2] Ref. 6, p. 164.

the anal series. The base throughout this family is pentagonal, and the basals number either five, four, three, or one. When five basals are present the basal sutures meet the radials in the normal manner. When four basals are present either the anterior or left anterior suture is missing, and when only three basals are present the sutures meet the anterior, left-anterior, and right-posterior radials.

The Calyptocrinidae have throughout a pentagonal base and only four basal plates, and the anal plates are entirely missing.

In considering these families the question arises as to whether the base has been pentagonal throughout its whole phylogenetic history or whether there has been a hexagonal stage, as in the Batocrinidae and Actinocrinidae.

The Platycrinidae and Hexacrinidae are characterized by having the ambulacral grooves and lower brachial plates but slightly incorporated in the calyx. The orals in the simpler forms are well developed, and the base is either pentagonal or hexagonal. In the Platycrinidae no anals have been positively determined, and the base is pentagonal. Throughout this group there are ordinarily but three basals, five in youth and sometimes but one in age. Two of the basals are large, the third smaller. In the *Hapalocrinus*,[1] the smaller basal is the right-anterior one, and the basal sutures meet the anterior, right-anterior, and the left-posterior radials, as in *Stephanocrinus*. In the other genera of Platycrinidae the left-anterior basal[2] is the smaller, and the basal sutures meet the anterior, left-anterior, and right-posterior radials. In the Hexacrinidae there are usually three, or two, equal basals, sometimes only one.[3] The base is hexagonal and the anal plate well developed. The basal sutures in the three-basal forms meet the antero-lateral radials and the anal plate; in the two-basal forms the sutures meet the anterior radial and the anal plate.

A discussion of the monocyclic Inadunata as a whole cannot now be undertaken, but certain species of Larviformia which in their development illustrate very clearly, even diagrammatically, some of the slighter morphological changes found in the Camerata will be considered in the discussion of morphological principles.

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[1] Ref. 21, pp. 94–110.

[2] Exceptions are noted on p. 507 in the description of Fig. 5, No. 6.

[3] Ref. 6, p. 158.

Having noted the more conspicuous changes through which the basal cup has passed, a detailed study of the processes involved in these may be undertaken.

DETAILED STUDY OF PROCESSES ACTIVE IN PLATE EVOLUTION

The processes active in the evolution of crinoid plates, especially the basals and radials, may be divided into two broadly separated though often co-operating groups: (1) those which do not *necessarily* modify the relation of contact and position of the plates; and (2) those which do modify these relations. The discussion of the first group of processes includes: (*a*) symmetrical growth; (*b*) symmetrical reduction; and (*c*) anchylosis. The second group includes: (*a*) reduction and compensating growth; (*b*) enlargement and compensating reduction; (*c*) plate division; (*d*) plate migration; (*e*) plate interpolation; and (*f*) anchylosis.

1. CHANGES NOT PRIMARILY MODIFYING THE RELATIONS OF PLATE CONTACT AND POSITION

a) *Symmetrical growth.*—Plate growth in the Echinoidea and Crinoidea[1] is due to the deposition, by amebod cells, of crystalline calcium carbonate, or calcium and magnesium carbonate[2] in reticulate pattern in the mesenchyme. Three, or perhaps more, of the ameboid calciferous cells fuse by means of pseudopodia into a plasmodium or reticulate tissue.[3] There the pseudopodia meet, the protoplasm forms a small calcareous nodule (intracellular secretion, according to Theel; extracellular, according to Semon), which gradually increases along the pseudopodia, forming a triradiate spicule. By further branching and anastomosis, the branches of the spicule meet and fuse at the tips of their processes (Fig. 3, No. 3), thus building up a hard tissue (stereom), showing a strongly reticulated structure (Fig. 3, No. 4) when sectioned in any direction. The co-ordination of deposition is such that each plate acts optically and mineralogically as a single crystal of calcite, without other planes of weakness than the cleavage planes developed by crystallization. The margins of the plates are at first rough with sprouting spicule branches (Fig. 2, No. 2, R), but later, upon coming into mutual contact, become smooth (Fig. 2, No. 5). Growth by branching and anastomosis gives way to interstitial growth,[1] and the increase in size is more gradual. Each plate, as it now enlarges, is carried relatively outward and away from the adjacent plates, and in the basal cycle not only away from the adjacent plates, but also away from the axial canal, as is shown by growth lines whenever present. When growth of the plates is symmetrical, each plate in a cycle is the equivalent in size and shape of every other plate in that cycle, and has the same angles with reference to the central axis of the cup as the other plates in the cycle.

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[1] Although no observations have been made upon the early details of plate deposition (stereom formation) in the Crinoidea, the growth of the plate from the primary spicule on so closely parallels that in the Echinoidea that there can be no doubt concerning the method of formation.

[2] Composition of crinoid skeletons: ref. 25, p. 31; ref. 14, p. 488; ref. 17.

[3] Stereom formation: ref. 34.

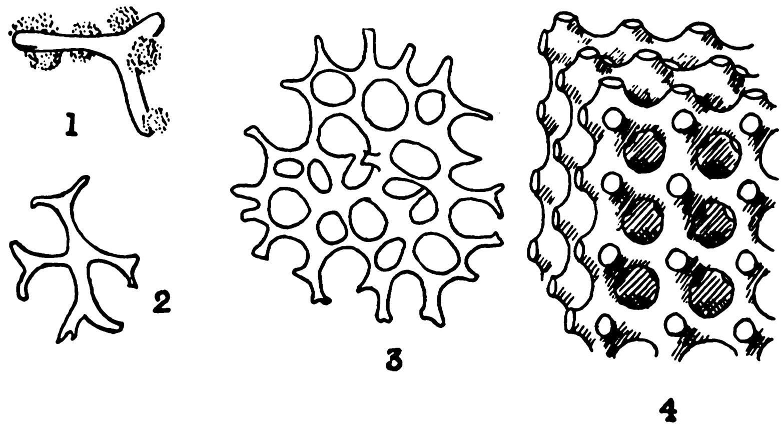

FIG. 3.—Stereom formation: 1, formation of the triradiate spicule by the fusion of seven calciferous cells; 2, basal from a larva of *Antedon* on the sixth day; 3, basal on the tenth day; 4, ideal representation of regular, reticulate stereom. (1, after Theel; 2, 3, after Bury; 4, after P. H. Carpenter.)

b) *Reduction of parts by absorption.*—This also is a function of ameboid cells, which are similar in appearance to the calciferous cells, but take the calcareous salts into solution and transmit them to the deposition cells.[1] When reduction by proximal or distal, or proximal and distal, absorption is symmetrical throughout a cycle of plates, the relation of parts is not disturbed, unless the reduction of the cycle is complete, thus bringing previously separated cycles into apposition with each other.

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[1] Ref. 35, p. 538.

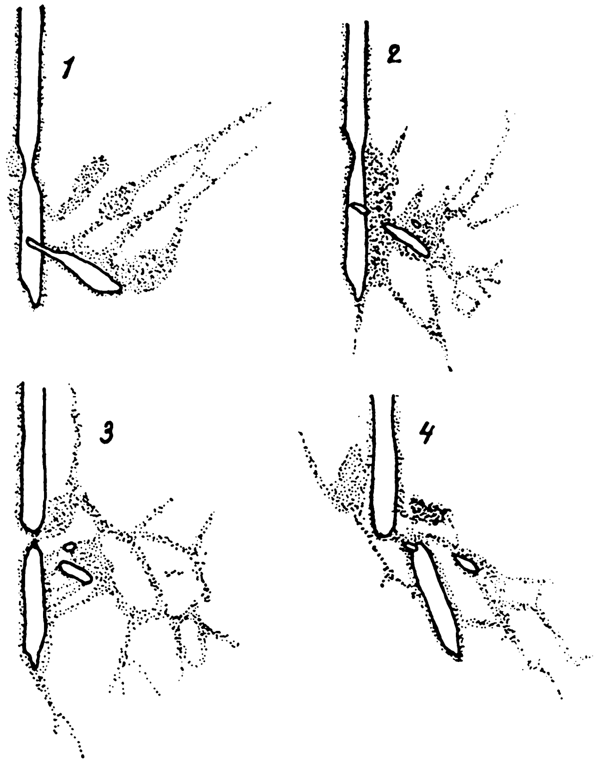

FIG. 4.—Stereom absorption; absorptive cells operating upon the posterior end of a calcareous rod in a mature pluteus: 1, one portion of rod separated, the second partially cut; 2–4, advancing stages up to the nearly completed absorption of portion one, the separation of portion two (after Theel).

c) *Anchylosis.*—Anchylosis is the uniting of apposed plates by an unbroken deposit of stereom in the sutures, and is, as far as we know, an ontogenetically repetitive process, taking place only between plates and not between their formative cell groups. The intrasutural deposit is formed through the activity of the ameboid, calciferous cells, and the firmness with which the plates are united depends upon the amount of stereom deposited. In youth the deposit is slight, the plates are easily separated, and the sutures are usually discernible as external or sometimes as internal grooves. In age, however, much variation exists, for the extent of deposition depends upon the stage of development reached by the group and upon the vitality of the individual. In some cases immature (incomplete) anchylosis is apparently an adult characteristic and the plates are easily separated.[1] In other cases the deposit is as strong as the stereom of the plates, and fracturing results as readily in the plates as in the old suture plane. Again, in cases where firm union is the rule, as in the Camerata, lowered vitality, or other physiological disturbance, sometimes results in the partial or total inhibition of anchylosis. Such abnormalities, or reversions, are of great value in determining the position of sutures otherwise untraceable, and will be more fully considered under the topic of delayed anchylosis.

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[1] Ref. 34, pp. 349–351.

From the foregoing definition of anchylosis the conclusion is drawn that any suture or group of sutures appearing in the primitive basal cup may be lost through anchylosis, and the following discussion will show the actual and possible combinations due to simple anchylosis alone.

In order to facilitate this description and the tabulation of the variations to be cosidered, the convention of lettering the basal plates from the posterior to the right-posterior, in an anticlockwise direction, has been adopted, the letters separated by dashes making up the basal formula. The letters from *a* to *e* denote the plates and the dashes the intervening sutures; a dash over a letter shows trunkation of that plate, while the absence of a dash between the letters denotes the absence of the suture between those plates. Thus, *a—b—c—d—e—* is the formula for the simple, pentagonal base while $\bar{a}$*—b—cd—e—* shows a hexagonal base with the posterior basal trunkated and the anterior pair of basals united.

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[1] Ref. 1, p. 29; ref. 10, pp. 36, 37.

From a study of Figs. 1 and 9 it will be seen that eight types of basal modification, by the reduction in number of the basal plates, occur in the Camerata during the Paleozoic era. The primitive base (*a—b—c—d—e—*), Fig. 1, No. 1, appears in the Ordovician, but it probably originated long before that time. The four-basal type (*a—b—cd—e—*), Fig. 1, No. 2, appears in the Ordovician, becomes abundant in the Silurian, and disappears before the close of the Devonian. The three- inequi-basal type (*ab—c—de—*), Fig. 1, No. 3, makes its appearance in the Ordovician, increases in the Silurian, reaches its climax in the Devonian, and disappears in the Mississippian. The three- inequi-basal type (*ea—bc—d—*), Fig. 1, No. 6, is present during the Silurian, Devonian, and Mississippian, but never becomes very prominent. The one-basal type (*abcde*), Fig. 1, No. 5, occurs at various times during the Paleozoic period, but not as a generic or specific characteristic. The hexagonal, five-basal type (*ā—b—c—d—e—*), Fig. 9, No. 6, is present in the Ordovician. The hexagonal, four-basal type (*ā—b—cd—e—*), Fig. 1, No. 8, appears first in the Silurian (Richmond) and disappears during the Silurian. The three- equi-basal type (*ab—cx—de—*)[1], Fig. 1, No. 10, appears in the Silurian, increases in the Devonian, reaches its climax in the lower part of the Mississippian, and then disappears. The two- equi-basal type (*abc—xde—*),[1] Fig. 1, No. 12, is introduced in the Kinderhook and becomes extinct in the lower part of the Pennsylvanian.

Possible combinations of the primitive five-basals: Since Wachsmuth and Springer have assumed that all crinoids having an unequally tripartite base have the smaller basal in the left-anterior interray, it may be well to consider what combinations may be expected from anchylosis of the primitive five-basals. These combinations are explained below and illustrated in Fig. 5.

Fig 5, No. 1, illustrates the primitive basal cup of pentagonal outline, represented by the formula *a—b—c—d—e—*, and found in *Glyptocrinus*, *Schizocrinus*, *Stelidiocrinus*, and young individuals of *Platycrinus*.

Fig. 5, No. 2, shows a common Ordovician and Silurian type of reduction (*a—b—cd—e—*), in which the two anterior basals are

[1] Formula based upon Wachsmuth and Springer's theory.

anchylosed. In this group there are five possible combinations: *ab—c—d—e—*, *a—bc—d—e—*, *a—b—cd—e—*, *a—b—c—de—*, and *ea—b—c—d—*. Of these combinations, *a—b—cd—e—* has been the only one described in the four-basal Melocrinidae; however, the writer has found the *a—bc—d—e—* (No. 2*a*) combination in the following specimens in the Springer collection: of eight specimens of *Melocrinus calvini* from Calloway County, Missouri, four could be properly oriented[1], and these showed the *bc* anchylosis (Pl. II, No. 4), as did two specimens of *M. obconicus* ? Hall, and one of the type specimens of *M. roemeri.* The other four-basal forms of the Melocrinidae(?) and the Eucalyptocrinidae[2] have the *a—b—cd—e—* type of base.

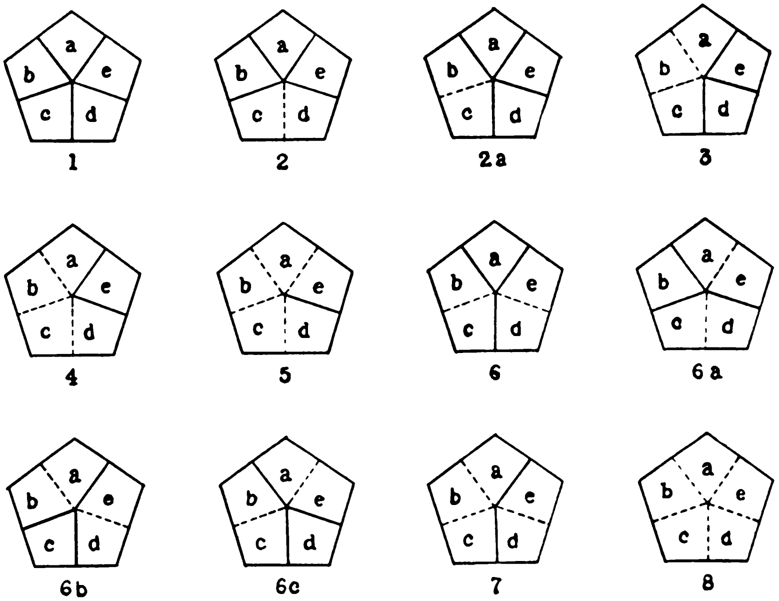

FIG. 5.—Diagrams illustrating types of the possible combinations due to anchylosis of two or more of the primitive five-basals.

Fig. 5, No. 3, illustrates a type in which three adjacent basals have been anchylosed (*abc—d—e—*). Here again five combinations are possible: *abc—d—e—*, *a—bcd—e—*, *a—b—cde—*, *b—c—dea—*, and *c—d—eab—*. Of these combinations one, the *abc—d—e—* combination, is found in *Zophocrinus*, as figured. This orientation does not agree with Bather's interpretation of the genus,[1] but is based upon the discovery of the anus in a large number of specimens studied by the writer in the Springer and Walker Museum collections.

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[1] In orienting these specimens the anal tube was used as the reference point.

[2] This orientation of *Eucalyptocrinus* is strictly arbitrary, as no indices for proper orientation have as yet been discovered.

Fig. 5, No. 4, shows the anchylosis of four adjacent plates (*abcd—e—*), leaving but one free plate. Here, however, any plate of the five might have been the free plate, and five combinations are possible: *abcd—e—*, *a—bcde—*, *b—cdea—*, *c—deab—*, and *d—eabc—*. Of these combinations none have been discovered.

Fig. 5, No. 5, illustrates one of five possible combinations in which only one suture exists (*abcde—*). Combinations 4 and 5 seem too asymmetrical from a structural viewpoint to occur as either generic or specific characters, but might appear in cases of delayed anchylosis, in which complete anchylosis is the normal result.

Fig. 5, No. 6, illustrates the simple tripartite combination (*ab—c—de—*), in which two pairs of basals are anchylosed. Of the five possible combinations of this type four are now known: *a—bc—de—*, in *Allagecrinus americanus*;[2] *b—cd—ea—*, in *Storthingocrinus*[3] and *Hyocrinus* (No. 6, *a*)[4]; *ab—c—de—*, in *Sybathocrinus* and the Platycrinidae (No. 6, *b*); *bc—d—ea—*, in *Hapalocrinus*[5] and *Stephanocrinus*[6] (No. 6, *c*). The fifth combination (*ab—cd—e—*) has not yet been discovered.

Fig. 5, No. 7, illustrates one of the five possible combinations in which three- and two-basals are anchylosed, as *abc—de—*, etc. Of these only one is known, *abc—de—* in *Mycocrinus*,[7] as figured.

Fig. 5, No. 8, shows the complete type of anchylosis (*abcde*). While this formula recognizes but one type of complete anchylosis, the type may have been derived by the simultaneous anchylosis of the five primary plates, or from the closure of the remaining sutures in any of the thirty possible combinations given above. Dealing here with results alone, we see that thirty-one possible modifications of the five primary basals are obtainable through simple anchylosis.

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[1] Ref. 6, pp. 150, 151.

[2] This combination was found recently, by the writer, in two specimens of *Allagecrinus americanus* in a large collection of that species made by Professor Weller at Louisiana, Missouri.

[3] Ref. 3, p. 426.

[4] Ref. 6, p. 153.

[5] Ref. 21, pp. 95–105, Pls. 9, 10.

[6] Ref. 19, pp. 212, 351.

[7] Ref. 28, p. 110, Pl. 7, Fig. 4.

[*To be continued*]

EXPLANATION OF PLATES

PLATE I

Teleiocrinus umbrosus Hall. Abnormal specimen cited by Wachsmuth and Springer as confirmation of their theory

No. 1.—Oblique view of posterior interray, showing absence of anal plate and one of the first interbrachials, and the reduction of the right-posterior basal. Basal formula, *ab—cd—e—*; formula of posterior interray, *o—1—3—4—2—*.

No. 2.—View of right-posterior interray, showing normal arrangement of interbrachials *1—2—2—2—*, and reduction of right-posterior basal.

No. 4.—Posterior view.

No. 6.—Tegmen, showing position of anal tube.

Teleiocrinus umbrosus Hall. Springer collection; normal specimens

Fig. 3.—Posterior view, showing normal posterior interray and normal base. Basal formula, *ab—cd—ex—*; formula of posterior interray, *A—2—3—4—1—*. To be compared with Nos. 1 and 4.

No. 5.—Tegmen, showing position of anal tube in another specimen; to be compared with No. 6.

PLATE II

Glyptocrinus decadactylus Hall. Springer collection, specimens having a pentagonal base

No. 1.—Basal view, showing normal pentagonal base with five basals. Basal formula, *a—b—c—d—e—*.

Chicagocrinus inornatus Weller (type). University of Chicago Paleontological Collection, No. 10787

No. 2.—Basal view, showing anchylosis and reduction of antero-lateral basals and compensating enlargement of postero-lateral basals. Basal formula, *a—b—cd—e—*.

Melocrinus calvini Wachsmuth and Springer. Springer collection

No. 3.—Posterior view.

No. 4.—Basal view of same specimen, showing anchylosis and reduction of sinstro-lateral basals and compensating enlargement of posterior and right-anterior basals. Basal formula, *a—bc—d—e—*.

Stephanocrinus angulatus Conrad. University of Chicago paleontological Collection, No. 10787

No. 5.—Basal view, showing anchylosis and reduction of right-posterior and posterior and sinstro-lateral basals, and compensating enlargement of right-anterior basal. Basal formula, *ea—bc—d—*. Note reduction of right-posterior and left-anterior radials.

Platycrinus subspinosus Hall. Springer collection

No. 6.—Basal view, showing normal *Platycrinus type of anchylosis.* Basal formula, *ab—c—de—*. To be compared with No. 5.

Abacocrinus tesselatus Angelin. Springer collection, specimens having a hexagonal base

No. 7.—Basal view, showing asymmetry of posterior radials, enlargement and trunkation of posterior basal, and anchylosis and reduction of antero-lateral basals, coupled with compensating enlargement of postero-lateral basals. Basal formula, *ā—b—cd—e—*.

Melocrinus sampsoni M. and G. (type). University of Chicago paleontological collection, No. 6958; probably *Actinocrinus chouteauensis* S.A.M.

No. 8.—Basal view showing reappearance of anterior basal suture. Basal formula, *ab—c—d—ex—*.

Batocrinus. University of Chicago paleontological collection No. 9082

No. 10.—Basal view of normal specimen. Basal formula, *ab—cd—ex—*.

No. 11.—Basal view of abnormal specimen, showing reappearance of anterior basal suture. Basal formula, *ab—c—d—ex—*.

Actinocrinus multiradiatus. University of Chicago paleontological collection No. 8959

No. 9.—Basal view with base removed, showing asymmetry and reduction of posterior radials. Compare with Nos. 7–14.

Steganocrinus pentagonus Hall. Springer collection

No. 12.—Basal view of normal specimen, showing asymmetry and reduction of posterior radials. Basal formula, *ab—cd—ex—*.

No. 13.—Basal view of abnormal specimen, showing loss of the antero-lateral and posterior basal sutures and the reappearance of the anterior and left-posterior sutures. Basal formula *bc—dea—*; factor *x* may or may not be present.

No. 14.—Basal view of another abnormal specimen, showing loss of right-anterior basal suture and reappearance of anterior suture. Basal formula, *ab—c—dex—*.

No. 15.—Basal view of abnormal specimen, University of Chicago paleontological collection, No. 8979, showing loss of anal plate. Basal formula, *b—cd—ea—*. See Plate III.

PLATE III

Steganocrinus pentagonus Hall

No. 1.—Posterior view of abnormal form of Pl. II, No. 15.

No. 2.—Tegmen of same specimen, showing position of anal tube.

No. 3.—Posterior view of normal specimen in Springer collection. To be compared with No. 1.

Hexacrinus elongatus Goldfuss. Springer collection

No. 4.—Basal view of normal form. Basal formula *ab—cd—ex—*.

Note reduction of posterior radials.

Hexacrinus anglypticus Goldfuss. Springer collection

No. 5.—Basal view of abnormal form, showing loss of posterior basal suture and reappearance of left-posterior suture. Anchylosis of anterior basals normal. Basal formula, *b—cd—ea—*; factor *x* may or may not be present.

No. 6.—Basal view of another abnormal specimen, showing loss of right-anterior basal suture and reappearance of anterior suture. Basal formula, *ab—c—dex—*.

Talarocrinus patei M. & G, Springer collection

No. 7.—Basal view of normal specimen. ×2. Basal formula, *abc—dex—*.

No. 8.—Basal view of abnormal specimen, showing reappearance of left-posterior basal suture. ×2. Basal formula, *a—bc—dex—*.

No. 9.—Basal view of another abnormal specimen, showing reappearance of left-anterior basal suture. ×2. Basal formula, *ab—c—dex—*.

No. 10.—Basal view of another abnormal specimen, showing loss of posterior basal suture and reappearance of left-posterior and right-anterior sutures. ×2. Basal formula, *bc—d—ea—*. Factor *x* may or may not be present.

Pterotocrinus cirnarius Lyon, Springer collection; Tegmen figured by Wachsmuth and Springer, ref. 39, Pl. LXXIX, Figs. 7*a*, 7*b*

No. 11.—Basal view, showing great reduction of anal plate, and asymmetry of posterior radials. Basal formula, *abc—dex—*.

Dichocrinus inornatus W. and Sp. Springer collection

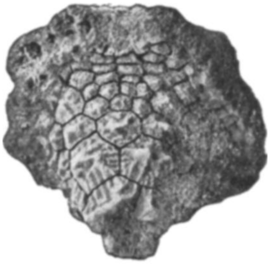
No. 12.—Lateral view of normal specimen. ×1½.

No. 15.—Tegmen of normal specimen showing flexible condition of anal tube and interambulacral areas. ×2.

Platycrinus symmetricus W. and Sp. Springer collection

No. 13.—Lateral view, showing similarity to No. 12. ×1½

No. 14.—Tegmen of young specimen, figured by ref. 39, Pl. LXIX, Fig. 1*c*. Note flexible condition of anal tube and interambulacral areas, and general similarity to No. 15. ×2.



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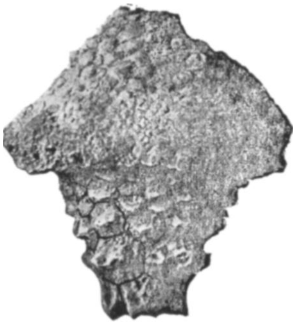

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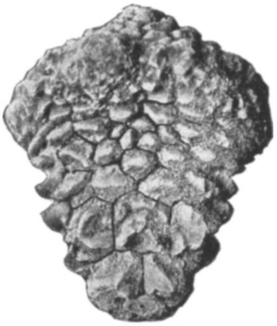

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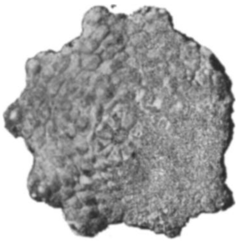

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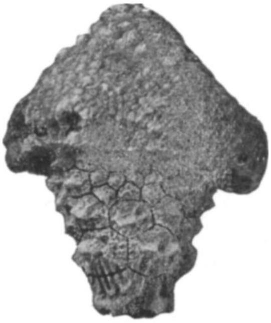

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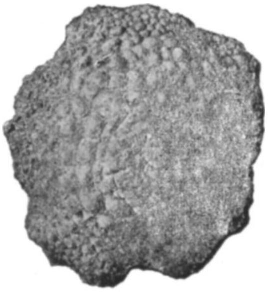

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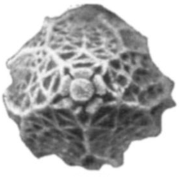

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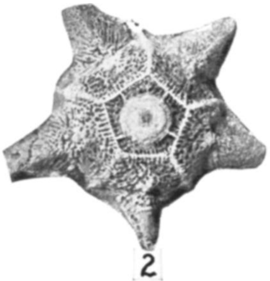

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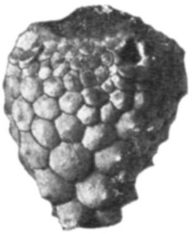

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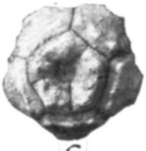

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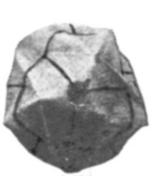

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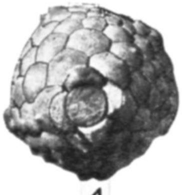

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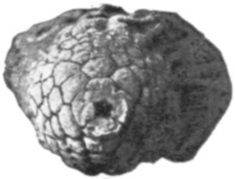

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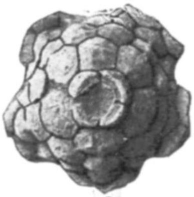

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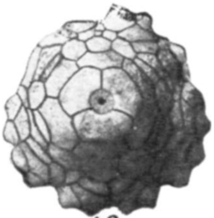

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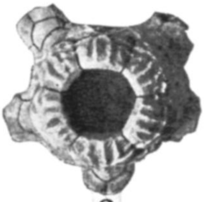

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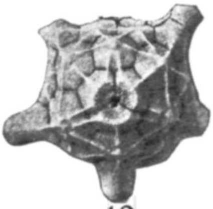

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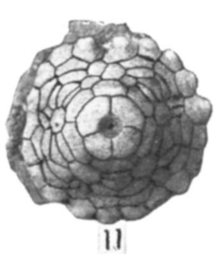

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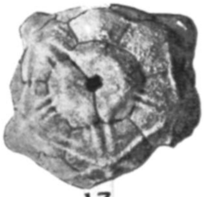

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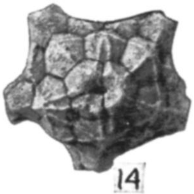

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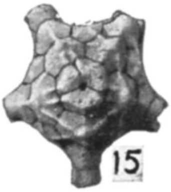

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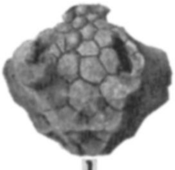
PLATE III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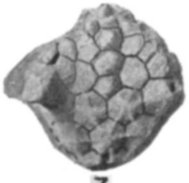
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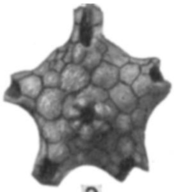
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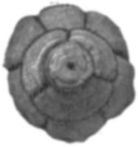
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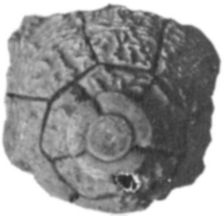
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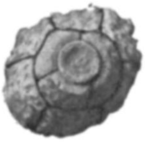
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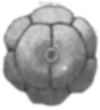
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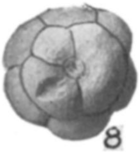
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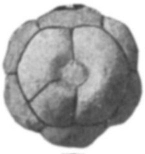
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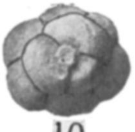
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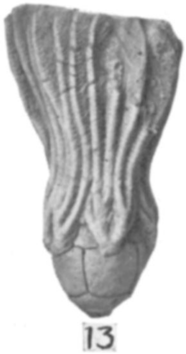
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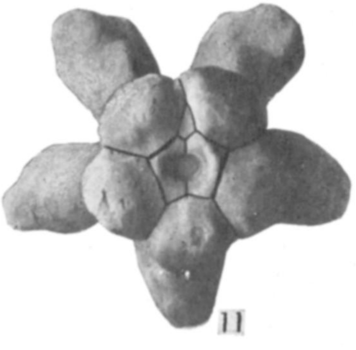
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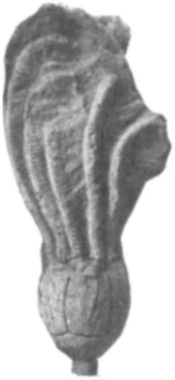
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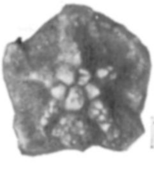
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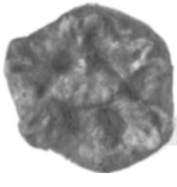
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